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Reduced Forage Access Affects Home Range Size and Site Fidelity of Svalbard Reindeer (*Rangifer tarandus platyrhynchus*).

Redusert mattilgang påvirker størrelsen på
leveområdet og graden av stedegenhet for
Svalbardrein (*Rangifer tarandus platyrhynchus*).

Christina Kinck

Preface

Firstly, I would like to thank my advisor, Professor Leif Egil Loe, for the opportunity to write this thesis and all the help during the process. The opportunity to visit Svalbard was irresistible and the field work in April was especially memorable. Thank you to the Research Council of Norway for the Arctic Field Grant, which covered the field work. And a huge thank you to Morten Meland for finishing the field work in August when I broke my ankle in the field, and also to Audun Stien, Roy Andersen, Bram van Moorter and Manuela Panzacchi for helping us. I also want to thank my parents and Jake Smith for all the patience and encouragement, as well as suggestions for improving the thesis.

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Abstract

The Arctic is currently warming and this trend is expected to continue. This will lead to increased frequency and spatial extent of rain on snow events which cause ground ice to form. In this extreme and marginal environment, ground ice can have detrimental effects on the species living there. The objective of this study was to investigate how environmental conditions impact seasonal variation in the home ranges of individually marked Svalbard reindeer, in terms of home range size and site fidelity. To accomplish this, GPS data from female Svalbard reindeer in three valleys on Svalbard was combined with information on seasons and icing events. Ground icing was determined based on data from ground temperature loggers, precipitation data and field data on ice thickness. Included in the study were two winters with icing events, 2009/2010 and 2011/2012, and two without, 2010/2011 and 2012/2013. Home ranges were calculated with a 95 % fixed kernel estimator and site fidelity was measured as percent overlap of seasonal polygon home ranges. The reindeer had larger seasonal home ranges and displayed less site fidelity during the winter than during the summer. Winter home ranges were larger during years with icing events, compared to winters without. There was no correlation between calf status and home range size or site fidelity, or between age and site fidelity. Animals aged four to seven years had larger home ranges than younger (2-3 years) and older (8-11 years) reindeer. Svalbard reindeer seem to use small ranges as long as there is enough forage. They expand their home ranges in search for forage due to variations of food accessibility caused by extreme weather events. In a warming Arctic, this behavioral plasticity may be able to buffer the effects of increased rain on snow events on a small spatial scale.

Sammendrag

Arktis er i ferd med å bli varmere og denne trenden forventes å fortsette. Dette vil medføre økt frekvens og utbredelse av regn på snø hendelser som forårsaker at is dannes på bakken under snøen. I dette ekstreme og marginale miljøet kan dannelse av ising på bakken ha skadelige effekter på artene som lever der. Målet med denne studien var å undersøke hvordan miljøforhold påvirker sesongvariasjon i leveområdene til individuelt merket svalbardrein, i form av leveområde og stedegenhet. For å oppnå dette ble GPS-data fra simler av svalbardrein i tre daler på Svalbard kombinert med informasjon om årstider og isingshendelser. Is på bakken ble fastsatt på grunnlag av data fra bakketemperaturloggere, nedbørsdata og felldata om tykkelsen på isen. Inkludert i studien var to vintre med isingshendelser, 2009/2010 og 2011/2012, og to uten, 2010/2011 og 2012/2013. Leveområder ble beregnet med en 95 % fast kernel estimator og stedegenhet ble målt som prosent overlapping av sesongmessige leveområdepolygoner. Reinen hadde større sesongleveområder og viste mindre stedegenhet om vinteren enn om sommeren. Vinterleveområder var større under år med isingshendelser enn under vintre uten. Det var ingen sammenheng mellom kalvestatus og leveområdestørrelse eller stedegenhet, eller mellom alder og stedegenhet. Dyr i alderen fire til sju år hadde større leveområder enn yngre (2-3 år) og eldre (8-11 år) rein. Svalbardreinen synes å bruke små leveområder så lenge det er nok fôr. De utvider sine leveområder på jakt etter fôr på grunn av variasjon i tilgangen på mat, forårsaket av ekstremvær. I et varmere Arktis kan denne atferdsmessige tilpasningen være i stand til å bufre effekten av ising på bakken på en liten romlig skala.

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1. Introduction

The Arctic is an extreme environment with marked seasonality, and it is a system that is sensitive to changes (Hinzman et al. 2005). The winters are long and cold, yearly precipitation rates are low and the annual solar cycle is highly skewed (Hinzman et al. 2005). It is evident that the terrestrial, freshwater, and marine systems in the Arctic are changing rapidly (Post et al. 2009), caused directly or indirectly by global climate change (Hinzman et al. 2005). The air temperatures of the Arctic in the 20th century are the warmest of the past 400 years, and has especially increased in the last 30 years (Serreze et al. 2000). Specifically, the annual average temperature on Svalbard has increased by 4.4 °C since the middle of the 1960s (Undelstvedt 2014). For resident species the warming could lead to better summer habitats, as earlier snow melt means that the plants can begin to grow sooner and the growing season will be longer (Hinzman et al. 2005). Warming of the Arctic could also lead to more frequent rain on snow events in the future (Liston & Hiemstra 2011; Rennert et al. 2009).

The rain on snow events can create ice layers on the surface, in the snow pack and on the ground, which can keep the animals from accessing forage (Rennert et al. 2009). Light rain or warm periods alone can block access to forage. In events with large amounts of precipitation the rain will percolate through the snow and freeze on the ground, creating ground ice, with the potentially largest impact on ungulates (Rennert et al. 2009). The timing of the icing events is also important. Early in the winter, icing events can lead to increased energetic costs for the animals over a longer time period (Rennert et al. 2009). Towards the spring when the animals are stressed, the cost of travel, reduced access to forage or increased risk of predation can increase mortality rates (Hinzman et al. 2005).

Burt (1943) stated that all mammals have a home range, which can be stationary or seasonally shifting. The simplistic view is that when young individuals find a suitable area they usually stay there for the rest of their lives, unless they are disturbed. The home range is usually defined as the area used by the animal for normal activities such as foraging, mating, and caring for their young, and occasional random trips do not count in the home range (Burt 1943). Home range sizes can vary depending on the sex, reproductive status and age of an animal, as well as season and population density. In particular, young animals are expected to have larger and less stable home ranges in their first years of life (Van Moorter et al. 2008) and females with calves are expected to have smaller seasonal home ranges than females without calves (Rettie & Messier 2001).

Some animals migrate between different home ranges for summer and winter, often due to spatiotemporal variation in food supply (Bischof et al. 2012). Migration can be caused by the food being inaccessible because of snow (Mysterud 1999) or ice (Stien et al. 2010). The tendency of an animal to return to previously used areas is termed site fidelity (White & Garrott 1990). Site fidelity has been documented for many species of birds and mammals (Greenwood 1980) and can influence the fecundity and survival of individuals, as well as population dynamics and demography (Hoover 2003). Advantages of familiar sites include knowledge of forage and predator avoidance (Greenwood & Harvey 1982), as well as possible mates and competitors (Shields 1984). There is a close link between home range and site fidelity. High overlap between home ranges used in two time periods is defined as high site fidelity, while a low overlap indicates migration or dispersal. Complementary analyses of home range sizes and site fidelity can be used to detect behavioral strategies (Rettie & Messier 2001).

One of the reindeer subspecies most at risk for population declines because of increased frequency and severity of extreme winter weather is the Svalbard reindeer (*Rangifer tarandus platyrhynchus*) (Vors & Boyce 2009). The Svalbard reindeer is an endemic Rangifer subspecies (Stien et al. 2010) inhabiting the Svalbard islands, therefore having limited dispersal possibilities (Vors & Boyce 2009). If the predicted increase of icing events holds true, it could prove detrimental for the Svalbard reindeer (Hansen et al. 2011; Stien et al. 2010). Depending on the spatial scale of the icing events and the behavioral strategies, the reindeer could enter a persistent population decline (Stien et al. 2010). It has been shown that warmer winter climate with more rain on snow events lead to more ice-locked pastures, which negatively affects the population growth rate of Svalbard reindeer (Hansen et al. 2011). There have been increased mortality and decreased population growth of reindeer on Svalbard caused by icing events in the past (Aanes et al. 2000; Kohler & Aanes 2004; Solberg et al. 2001). Nevertheless, Svalbard reindeer may be able to buffer the effect of ground icing by temporary emigrating from ice-locked pastures (Stien et al. 2010).

Tyler and Øritsland (1989) conducted a study on five individually marked and radio-collared Svalbard reindeer. They suggested that Svalbard reindeer appear to use small, traditional, seasonal home ranges and do not migrate over long distances or act nomadic within seasons. Reindeer on the west coast of Svalbard display partial migration between seasonal home ranges with a marked difference in the amount of forage (Hansen et al. 2010b). This supports the notion that the survival is mostly determined by the foraging conditions

during the winter (Aanes et al. 2000; Hansen et al. 2010b; Kohler & Aanes 2004; Solberg et al. 2001).

Although there have been studies conducted on the reindeer and their home ranges, the possible link between food restriction and home range size has not been investigated, as well as the effects of age and calving status. The objective of this study was to investigate how environmental conditions impact seasonal variation in the home ranges of 39 individually GPS-collared Svalbard reindeer. I predict that lower availability of food during winters would lead to a larger seasonal home range in winters compared to summers (P1a) (Tyler & Øritsland 1989) and larger seasonal home range in winters with icing compared to winters with less ground ice (P1b). Because food distribution may also be less predictable in winter due to annual variation in distribution of snow and ice, I predict that reindeer have higher site fidelity, or overlap between years, in summer compared to winter (P2a) and a lower degree of site fidelity in winters with icing compared to winters with less ice (P2b). Finally, I predict that the size of the home range and the degree of site fidelity depends on individual age (P3a) and calving status (P3b), with younger animals having larger home ranges (Van Moorter et al. 2008) and lower site fidelity, and females with calves having smaller home ranges (Rettie & Messier 2001) and a higher site fidelity. This is based on the observations that adult animals (Pettorelli et al. 2003) and females with calves are more stationary (Hiller et al. 2008).

2. Material and methods

2.1 Study area

The study area consists of the three valleys Reindalen, Colesdalen, and Semmeldalen, and their adjacent side valleys, which are all located on Nordenskiöld Land (78°N, 15°E) in Svalbard (Figure 1). The wide, supine valleys are surrounded by steep mountains and glaciers (Colman et al. 2001). The area is characterized by diverse vegetation, from polar desert with low plant cover to fairly dense marshes (Veiberg et al. 2007).

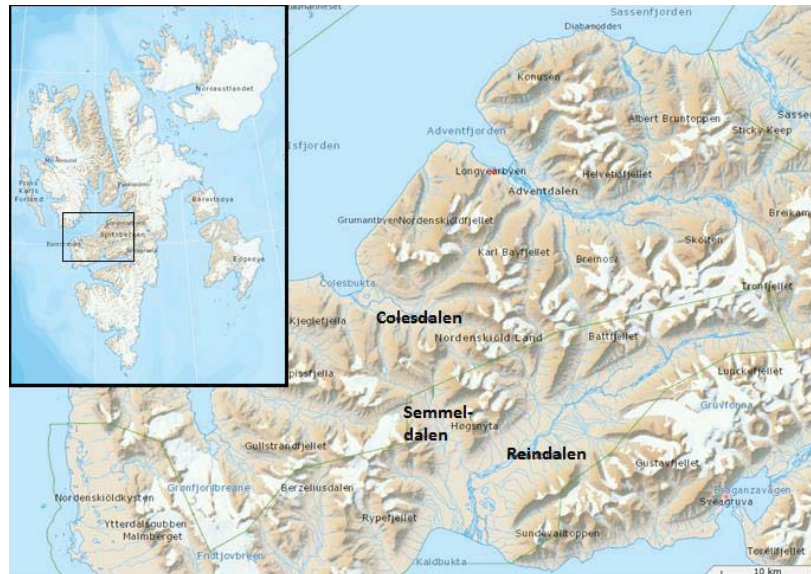


Figure 1. Map of the study area on Svalbard, which consists of the three valleys Colesdalen, Semmeldalen and Reindalen and their side valleys (The Norwegian Polar Institute).

The polar night, meaning that the sun is below the horizon around the clock, lasts from the middle of November through January (Statistics Norway 2012). The midnight sun with continuous daylight lasts from April 20 to August 22 (Statistics Norway 2012). The ground is covered by snow from October to June and frozen most of the year. This leads to a short growing season for plants of about six to eight weeks, which normally starts in the middle of June (Halvorsen & Bye 1999). The end of the growing season is usually early in September, when average temperatures are below zero (Van der Wal et al. 2000).

Svalbard typically gets a yearly precipitation between 200 and 400 mm, with the areas around Longyearbyen being the driest with between 150 and 230 mm of precipitation every year (Statistics Norway 2012). Most of the precipitation falls as snow during the winter (October to June) (Albon et al. 2002). In the last few decades, temperatures have been increasing in Svalbard, with melting glaciers and less precipitation during the winter (Statistics Norway 2012). The average temperature (1961-1990) is -16°C in the winter and

6°C in the summer (Statistics Norway 2012). The winter is characterized by low temperatures and strong winds (Nilssen et al. 1984), with warmer periods due to the oceanic influence (Halvorsen & Bye 1999). These warm periods are always followed by long periods of below freezing, which results in a layer of ice on the reindeer's forage areas (Hansen et al. 2011).

2.2 Study species

The Svalbard reindeer is a subspecies of reindeer which only live on the Svalbard islands, further north than any other cervid population (Aanes et al. 2000). They do not have any natural predators, though there have been rare cases where polar bears (*Ursus maritimus*) have killed Svalbard reindeer (Derocher et al. 2000). There is no interspecific competition (Hansen et al. 2011) as they are the only large herbivore on Svalbard (Loe et al. 2007). The reindeer came close to extinction because of extreme hunting pressure and became protected in 1925 (Reimers 1983). The hunting pressure on the reindeer is generally low today with an annual offtake of around 150 from a total population of about 11 000 reindeer (Sysselmannen på Svalbard 2009). They are usually thought of as sedentary (Tyler & Øritsland 1989), unless restricted access to forage forces them to move (Stien et al. 2010). The sedentary behavior is believed to be caused by the lack of competitors, predators, and harassing insects (Halvorsen & Bye 1999). The low availability of food sources and cold climate means that a more stationary behavior also helps conserve energy (Halvorsen & Bye 1999) and they spend up to 45 % of the day lying (Cuyler & Øritsland 1993).

The Svalbard reindeer's small body size is probably due to the low amount of available plant biomass in the Arctic (Van der Wal et al. 2000). In a study on the body composition of the Svalbard reindeer, Reimers et al. (1982) found that the animals have large digestive tracts and fat depots, as they spend most of their time grazing or resting, without being disturbed by insects or predators. The maximum concentration of body fat was higher for Svalbard reindeer than any reported values for other cervids, including domestic reindeer (Reimers et al. 1982). Other cervid species have evolved with predators, and therefore have to balance between storing enough fat to survive winters and being fast enough to escape predation (Reimers et al. 1982). The authors concluded that the Svalbard reindeer have adapted to a sedentary life in an environment without insect harassment or predators, but where the winters are harsh with reduced quantity and quality of food (Reimers et al. 1982).

Svalbard reindeer have higher activity levels in summer compared to winter (Loe et al. 2007). The reindeer are less active during periods with low temperatures and high precipitation during the winter (opposite during summer) (Loe et al. 2007). This might be

because the animals try to reduce heat loss in the cold temperatures by hiding from the weather or because the snow makes food less available (Loe et al. 2007). The coastal plains and valleys are important summer pastures, but in the winter these areas are mostly covered by snow, and some years by ice (Reimers 1983). Because of the marked differences between seasons, the reindeer have to use the vegetation effectively (Van der Wal et al. 2000). They depend on the short summer to restock their body reserves for the rest of the year, when most of the forage is buried under snow and ice, except the wind swept ridges (Van der Wal et al. 2000), slopes and high plateaus (Reimers 1983). Both energy and protein stores need to be refilled early in the year, after the harsh winter, especially for lactating females. Closer to winter the reindeer need to accumulate body fat to survive the winter. Van der Wal et al. (2000) found that reindeer graze selectively in areas with early snow melt, thereby selecting higher plant biomass and lower plant quality. Further, selecting plant biomass over plant quality probably maximizes the uptake of nitrogen and energy at the same time. Plant quality is important in temperate regions, but plant quantity is probably more important in the arctic, due to the low levels of plant biomass and high quality forage (Van der Wal et al. 2000). The selection for high biomass over plant quality probably leads to a better uptake of nitrogen and energy for the reindeer (Van der Wal et al. 2000).

Several studies have found that annual variation in population growth and density of reindeer are mostly influenced by annual variation in winter climate, probably because winter precipitation makes the forage unavailable for the reindeer. It could be either because the forage is covered or because the cost of movement is increased (Aanes et al. 2000). Aanes et al. (2000) found no effect of summer climate. Most carcasses in a mortality study were found on ridges, hillsides and plateaus (Reimers 1983), where the reindeer go in search of food during the winter. Most of the reindeer died during the winter, most likely during spring, from starvation (Aanes et al. 2000; Reimers 1983; Solberg et al. 2001). During winter, the number of days with heavy rain on snow events increased the proportion of pastures that were unavailable due to ice (Hansen et al. 2011). This had a negative effect on the population growth rates, also after accounting for animal density, likely due to increased mortality rather than migration (Hansen et al. 2011). Their model predicts that these events will become more common in the future, reducing the reindeer's access to forage during winter (Hansen et al. 2011). Stien et al. (2010) showed that winter icing events caused the reindeer to immediately search for available forage elsewhere. They stated that the effect of the icing events will likely depend on their spatial scale. If the forage is only covered by ice locally, the displacement of the reindeer searching for forage would reduce the mortality caused by the icing events. If

icing occur on a larger scale, the reindeer may not be able to escape through emigration (Stien et al. 2010).

The breeding season or rut is in October, and most of the calves are born during the first half of June (Omsjø et al. 2009). Winters with heavy precipitation and/or ice lead to reduced body conditions for females, which may explain the low recruitment rates the following year, which also explains the large variation of calf recruitment (Solberg et al. 2001). Calf production is negatively related to the total precipitation during winter (Albon et al. 2002). A study on Svalbard reindeer mortality found that most of the dead calves found had died during the winter, between the ages of six and twelve months (Reimers 1983). Solberg et al. (2001) found that the populations in the study areas show comparable growth rates and calves per female, indicating that the conditions in the valleys are similar.

2.3 Data collection

2.3.1 Reindeer

Adult female reindeer were captured and fitted with Vectronics aerospace GPS collars (850 g, approx. 1 – 2 % of the animal's winter weight) in February and April each year from 2009 to 2013, using methods approved by Sysselmannen and the ethics committee. These animals had been captured as calves in previous studies and marked and are therefore of known age (range: 2 – 11 years, Table 1).

Table 1. Number of animals of each age class. Each animal is followed over several years and therefore contribute with data in several age classes.

Age class	2	3	4	5	6	7	8	9	10	11
IDyear	7	12	8	13	13	16	14	5	3	1

The animals were captured using snow mobiles and manually restrained (Omsjø et al. 2009). While restrained, the calves were ear-tagged and collared with a plastic collar. For the animals marked for the purpose of this study, the old plastic collar was taken off and a new GPS-collar put on. The GPS data was downloaded from the collars after retrieval. The data is from a total of 39 individuals most often tracked over several years (n = 25 in 2009-2010, n = 33 in 2010-2011, n = 28 in 2011-2012, and n = 15 in 2012-2013), totaling 101 animal-years. Calving status was determined by visual observation of presence of calf-at-heel during a census in August where animals are located visually along census transects or by using VHF-tracking (Table 2). Not all GPS-marked animals were observed in summer.

Table 2. The number of observed animals that did or did not have a calf for each year.

Year	2009	2010	2011	2012	Sum
Calf	7	6	4	5	22
No calf	5	4	2	1	12

2.3.2 Icing events

Ice is formed when a period of above zero degrees Celsius is followed by freezing. Some years have more icing events than others, and this was determined based on the data from the collected temperature loggers, field validation data and precipitation data. A total of 128 temperature loggers (ibuttons) were placed in the study area in August 2009, and data was collected in August yearly between 2010 and 2013. They were placed in a water proof capsule and pressed about 5 mm into the soil, and therefore recorded the soil temperature. The loggers were marked with a 10 x 10 cm aluminum plate with the logger's number, and the position was recorded in a GPS unit. The loggers record the temperature every six hours throughout the year. In April 2010, February and April 2011 and 2012 and April 2013, snow depth (using shovel), ground ice (using axe), and layers of ice and hard snow were recorded near the loggers. They were located by GPS, a hole was dug and the measurements were done with a ruler. The precipitation data was collected at Svalbard airport in Longyearbyen by the Norwegian Meteorological Institute (www.eklima.no).

2.4 Statistical analyses

2.4.1 Icing events

Several data sets were combined to determine if a winter should be characterized as a winter with icing events or not, and the timing of the events. This included the data collected with the ground temperature loggers, in addition to field data and precipitation data. In order to estimate the probability of temperatures being 0°C or higher during the winter, I fitted Generalized Additive Models (GAM) using the gam function in the mgcv package (Wood 2006) with the R software (R Core Team 2013). The response variable was the sign of temperature (positive=1, negative=0) and the predictor was the date of the temperature measurement. Errors were assumed to be binomially distributed. With GAM, the curve is smoothed with splines, where one smoother is estimated at a time with the back-fitting algorithm (Zuur et al. 2009). Annual differences in mean ground ice thickness were analyzed for significance using t-tests.

2.4.2 Home range

The home range sizes were calculated using the kernel method (Worton 1989). The kernel method has been found to produce accurate estimates when analyzing home ranges (Seaman & Powell 1996). The size of the home ranges for the 39 reindeer were calculated using the “kernelUD” function in the R package adehabitat (Calenge 2006). The href smoothing factor (Worton 1989) was initially calculated independently for all individuals. Thereafter, the final Kernel home range was calculated using the mean smoothing factor for all individuals. Before the statistical analyses, the home range sizes were transformed to logarithmic values to reduce the effect of very large home ranges. A linear mixed effects model was fitted using the lmer function in the R-Package lme4, with log home range as the response variable, season, age or calving status as the explanatory fixed-effects variables, and individual as the random effect. Seasons were defined with winter as November 2 to May 31, calving from June 1 to June 30, summer from July 1 to September 14, and rut from September 15 to November 1. Age was classified into three groups; young (2 – 3 years), midlife (4 – 7 years) and old (8 – 11 years).

2.4.3 Site fidelity

I define site fidelity as the percentage overlap between seasonal 95 % minimum convex polygons (MCP). MCP was used in this context because they always produce one polygon (kernel can produce several) and for technical simplicity (existing function in R for calculating the overlap of MCPs but not for kernels). Site fidelity was investigated to determine if summer ranges are more stable than winter ranges. All animals with more than one season of GPS data were used (n=35 for winter and n=25 for summer). Overlap between home ranges was calculated separately for winter and summer and the polygon home ranges were mapped together with reindeer GPS-locations to visually confirm accuracy. The analyses of site fidelity was done with a linear mixed model with the percentage overlap between seasonal home ranges as the response variable, season (summer or winter), icing status (winters with ice compared to winters without ice), calving status or age (same groups as above) as fixed-effects variables (in different models) and individual as random effect.

For all the fixed effects in the mixed models I provide the confidence limits around the estimates. The effect of a variable is considered significant if the range of the 95 % confidence interval does not contain zero.

3. Results

3.1 Icing events

The field validation data showed a significant difference in ground ice thickness, with more during the winters of 2009/2010 and 2011/2012, than during 2010/2011 and 2012/2013 ($t=-22.3$, $p < 0.001$; Figure 2). The mean values for ground ice were 3.2 cm (\pm SD; 3.3) in 2009/2010, 0.3 cm (\pm SD; 0.9) in 2010/2011, 5.2 cm (\pm SD; 3.7) in 2011/2012, and 0.1 cm (\pm SD; 0.3) in 2012/2013. Therefore, the winters of 2009/2010 and 2011/2012 are termed winters with icing events, and the winters of 2010/2011 and 2012/2013 are termed winters without icing events.

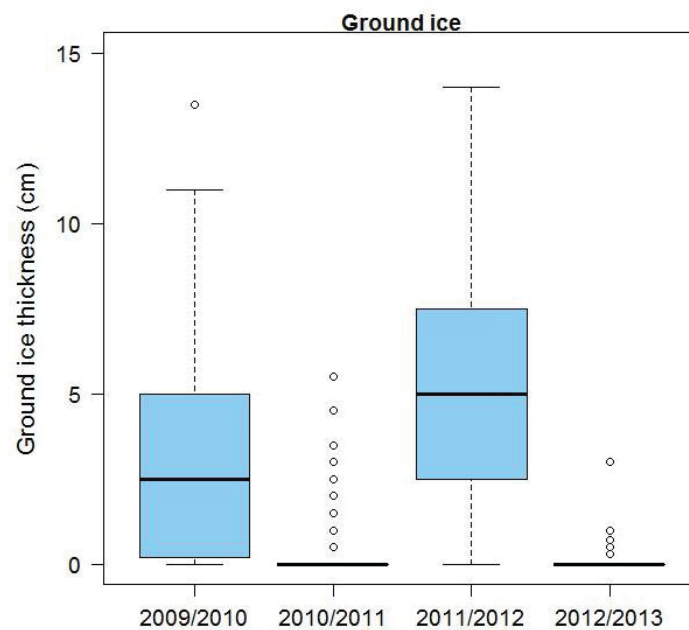


Figure 2. Box plots of ground ice formation measured in the field at the temperature logger locations. The black horizontal lines in the center of each box represents the median thickness of ground ice for each winter was (2.5 cm, 0 cm, 5 cm and 0 cm respectively), while the upper and lower part of the blue boxes represents 25 and 75 % quartiles.

There were two periods with temperatures above 0°C with precipitation during the winters of 2009/2010 and 2011/2012 (Figures 3 and 4). Most of the ground ice was probably formed in January/February both winters, when there was a high amount of precipitation combined with a warm period. On January 18 2010, there was 16.9 mm of precipitation and on January 30 2012, the precipitation measured 25.9 mm. Ice could also have formed in December of 2009, which had a warm period one day with 11.3 mm of precipitation. The winters of 2010/2011 and 2012/2013 had a few short warm periods with some precipitation.

Most of the precipitation these years fell as snow and did not lead to icing events, as is evident from the field measurements.

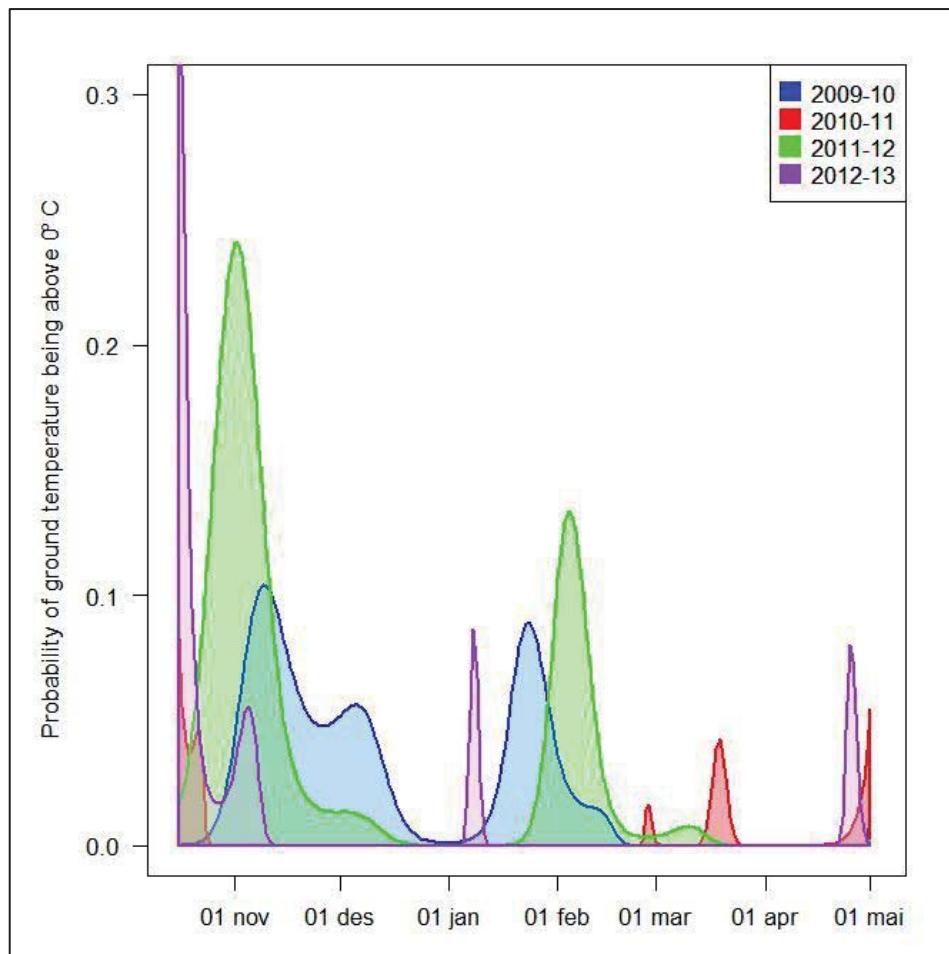


Figure 3. The probability of the temperature exceeding 0°C during each winter based on data from the ibuttons temperature loggers, from October 15 to May 1 for each year.

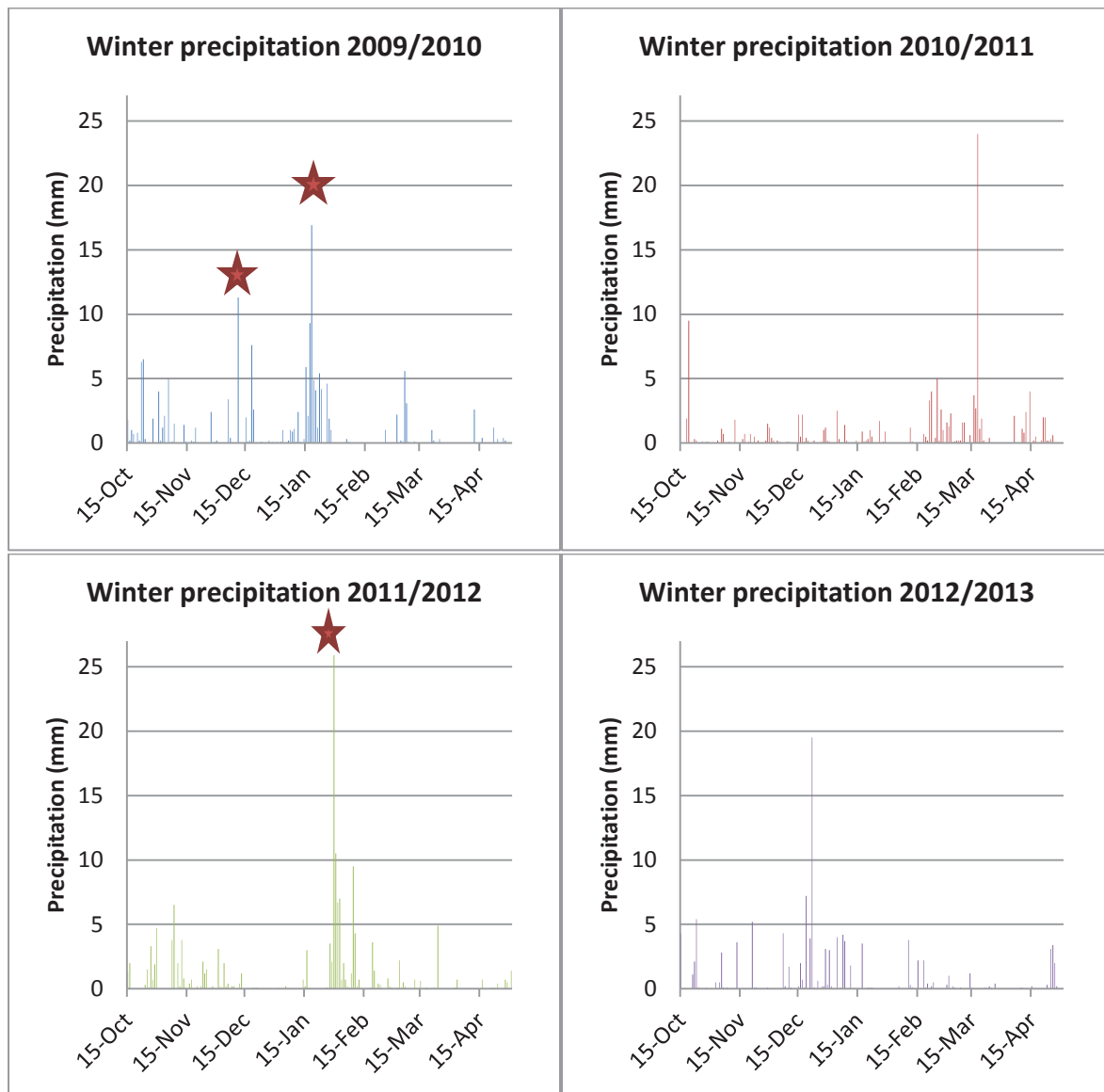


Figure 4. Daily precipitation during each winter (October 15 to May1) for the study period from www.eklima.no. The stars indicate dates of critical events.

3.2 Home range

Winter home ranges were significantly larger than summer home ranges (estimate of difference in log home range = 0.18 [95% CI: 0.06, 0.30]). The average size of a summer home range was 24.4 km² [range: 7.1km² to 60.9 km²] and the average size of a winter home range was 29.2 km², [range: 8.9 km² to 98.5 km²] with a difference of 4.8 km². The median values were 25.8 km² for summer and 30.7 km² for winter (Figure 5).

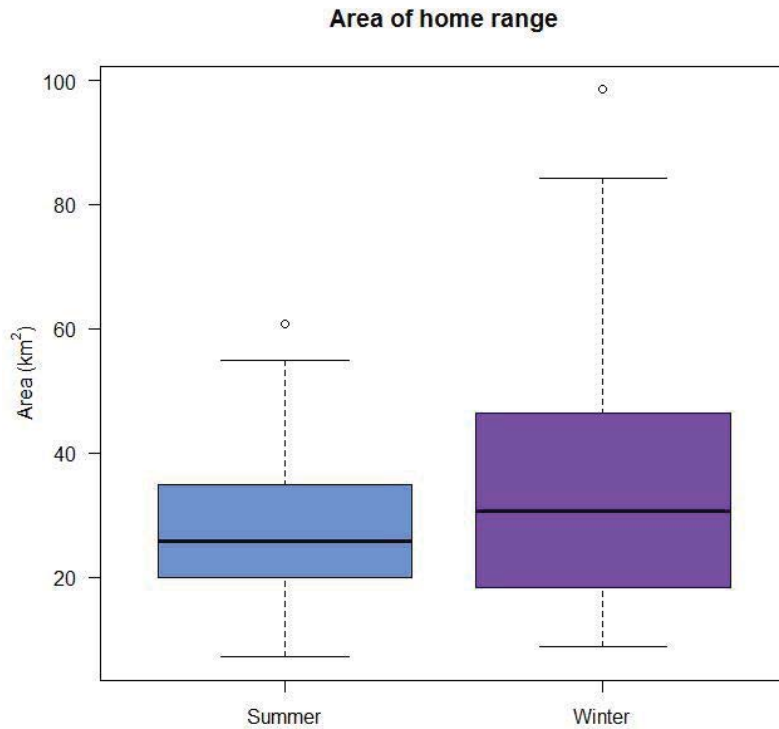


Figure 5. The area of 95 % kernel home ranges during the summer (blue) and during the winter (purple) for female Svalbard reindeer.

The size of winter home ranges during years without icing was significantly smaller than during years with icing events (estimate = -0.28 [95% CI: -0.43, -0.12]). The average size of a home range during years with icing events was 33.7 km² and the average size of a home range during years without icing events was 25.6 km², with a difference of 8.1 km². The median values for the winters with ice, 2009/2010 and 2011/2012, were 39.1 km² [range: 11.8 km² to 98.5 km²] and 37.1 km² [range: 8.9 km² to 80.7 km²], respectively. The median values for the years with less ice formation, 2010/2011 and 2012/2013, were 25.0 km² [range: 10.7 km² to 69.5 km²] and 22.8 km² [range: 10.9 km² to 49.5 km²], respectively (Figure 6; all the winter home range sizes are listed in Table 3 in the appendix).

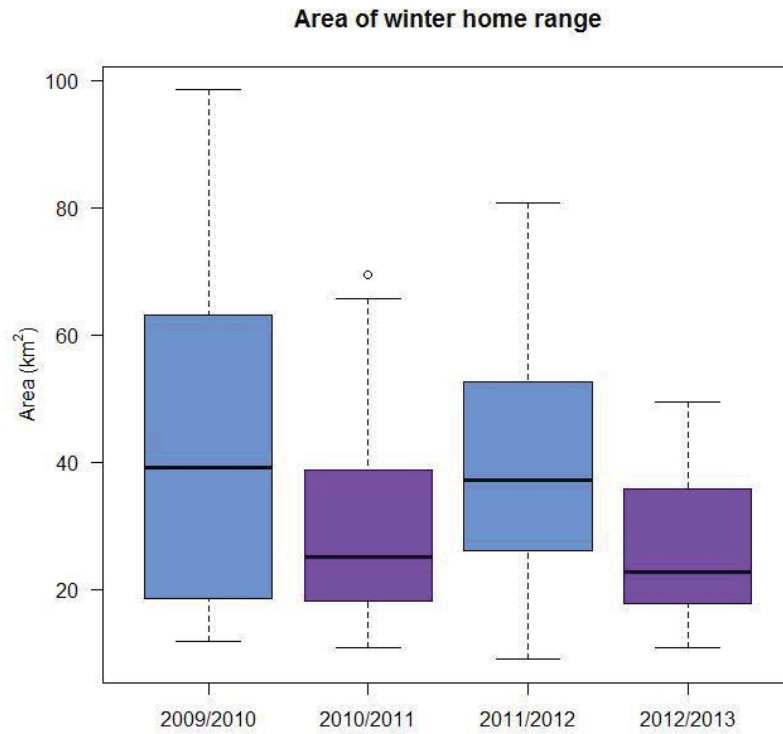


Figure 6. The area of kernel home ranges each winter. Purple are non-icing and blue are icing years.

Kernel home ranges for one individual followed over all 4 winters provide an example of the difference between icing and non-icing winters (Figure 7).

The average home ranges during summers and winters without icing events were very similar; 24.4 km² and 25.6 km², respectively.

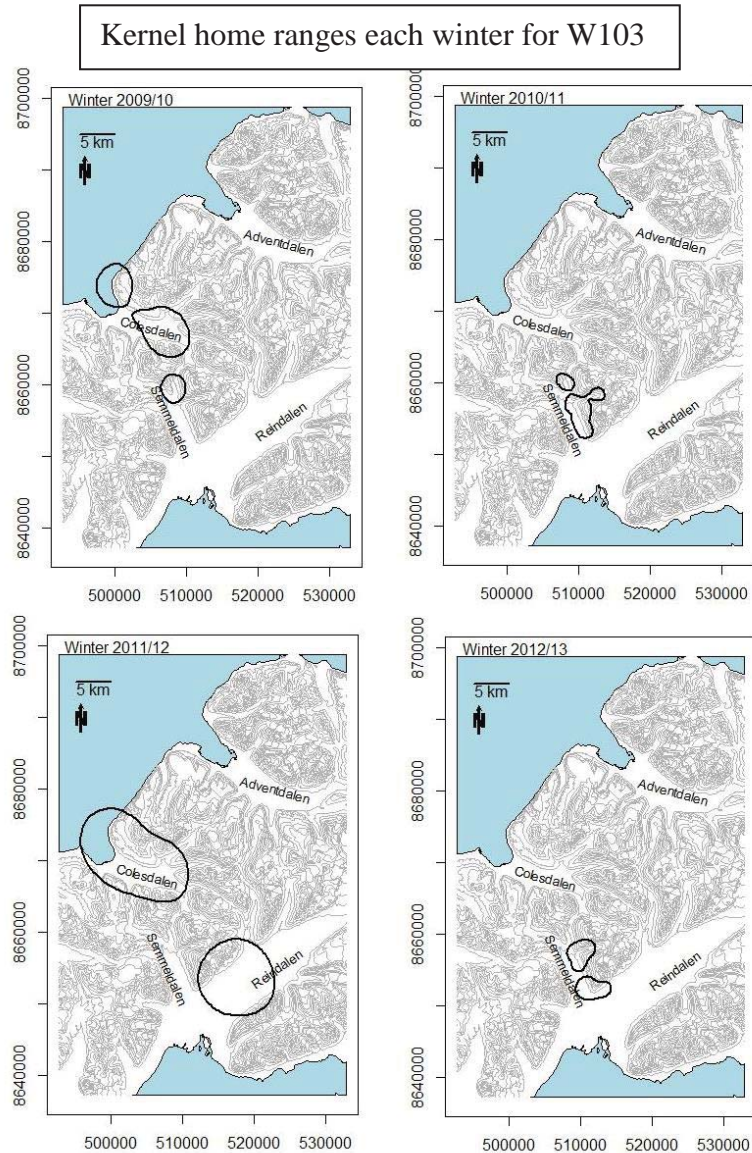


Figure 7. The 95% kernel home ranges of the individual female Svalbard reindeer W103 for each winter during the study period, illustrating the impact of icing on home range size. Icing years on the left (2009/2010 and 2011/2012) and non-icing years on the right (2010/2011 and 2012/2013).

The home range sizes of reindeer aged four to seven years (termed midlife) were marginally larger compared to the younger (estimate = -0.44 [95 % CI: -0.85, -0.03]) and older (estimate = -0.28 [95 % CI: -0.55, -0.02]) when tested with the whole year. Average values for the different ages were: midlife 48.9 km² [range: 10.5 to 114.5 km²], young 31.6 km² [8.5 to 100.7 km²], old 36.8 km² [10.2 to 92.8 km²]. The sizes of home ranges for each year-class are provided in Table 4.

Table 4. The median home range size of different aged Svalbard reindeer.

Age group	Young		Midlife				Old			
Age	2	3	4	5	6	7	8	9	10	11
Area (km ²)	42.1	30.2	63.4	70.6	62.7	48.2	31.2	24.2	46.9	17.5

There was no significant difference for the size of home ranges for reindeer with calves and reindeer without calves, neither when tested with the whole year (estimate = 0.13 [95 % CI: 0.50, -0.24]) or three of the seasons (summer: estimate = 0.08 [95 % CI: 0.35, -0.19], rut: estimate = -0.03 [95 % CI: 0.26, -0.32], winter: estimate = 0.16 [95 % CI: 0.51, -0.19], but with a strong tendency for a smaller home range during calving: estimate = -0.19 [95 % CI: 0.08, -0.46]).

3.3 Site fidelity

The overlaps of individual reindeer's home ranges during winter were significantly less than during summer (estimate of difference in percent = -17.4 [95% CI: -28.04, -6.76]). Summer home range overlap was on average 71 % [range: 20 % to 100 %] and winter home range overlap was 54 % [range: 0 % to 100 %]. The median values were 79.5 % and 46.0 % for summer and winter, respectively (Figure 8; exemplified by two animals in Figure 9).

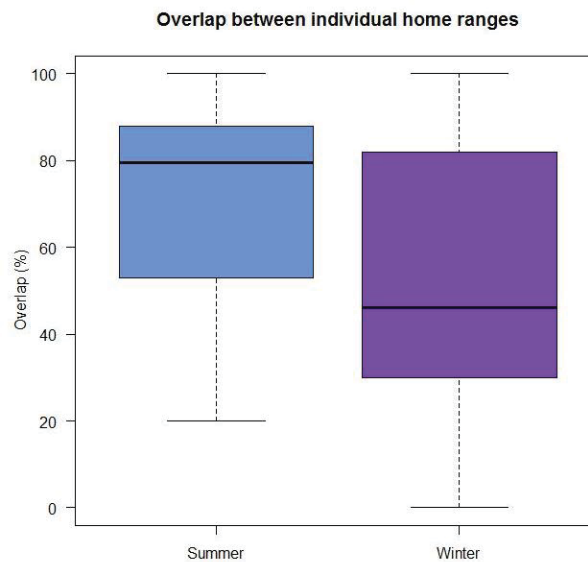


Figure 8. The overlap in per cent between individual polygon home ranges for female Svalbard reindeer for summer (blue) and winter (purple).

Polygon home ranges during summer and winter for two reindeer

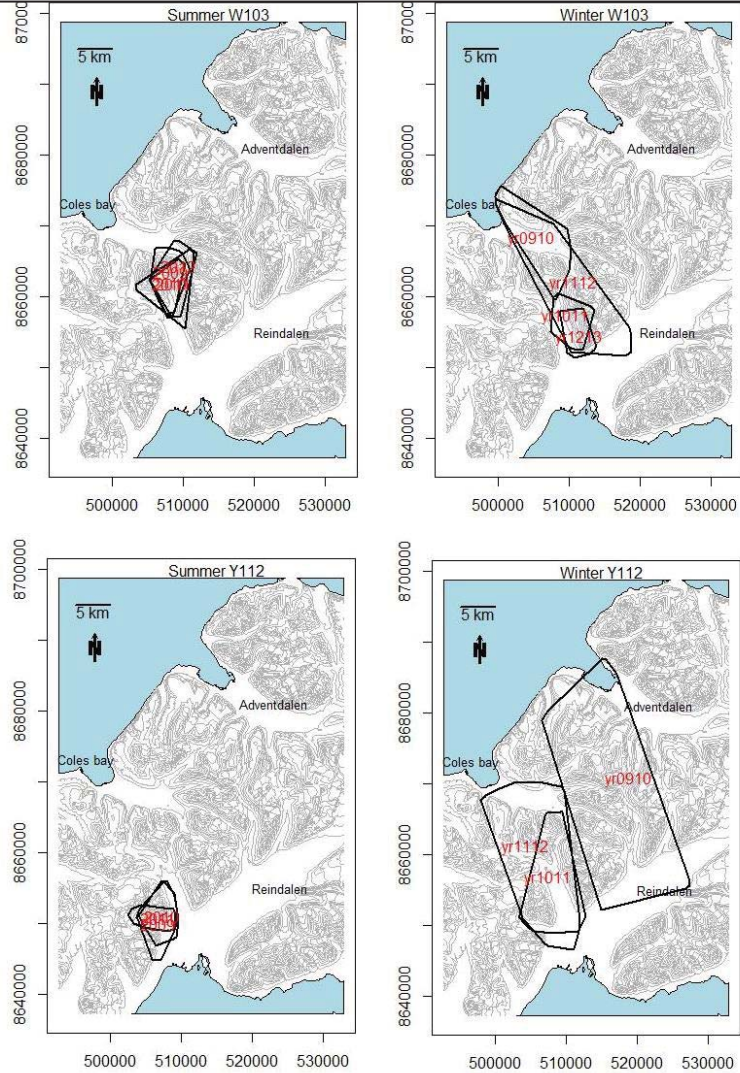


Figure 9. Polygon home ranges for two female Svalbard reindeer, W103 (top) and Y112 (bottom), during the summer on the left and during the winter on the right.

There was only a tendency for a smaller overlap of home ranges in icing years compared to non-icing years during winter (estimate = -13.17 [95% CI: -28.75, 2.40]). There was not a significant difference in overlap for different aged reindeer for summer and winter (estimate = 1.18 [95% CI: 4.16, -1.80]). There was borderline significance for a larger home range overlap in years they had calf compared to years without calf for both summer and winter (estimate = -18.69 [95% CI: -0.27, -37.11]). The average overlaps for years with calves and for years without calves were 75.7 % [range: 26 to 100 %] and 57.0 % [range: 0 to 100 %], respectively.

4. Discussion

Svalbard reindeer expand their home ranges to counter reduced forage availability during the winter, and especially during winters with icing events. Further, they display lower site fidelity during the winter to offset lower predictability of food. It is therefore apparent that arctic ungulates respond to critical climatic events by adjusting their range use. The results in this thesis are in accordance with a previous thesis, as they are based on the same data. Nedberg's (2012) study only had data for two winters and could not determine if the reindeer moved out of their home ranges in response to icing, as indicated by Stien et al. (2010). In this study, there is more data on reindeer movement for the two years included in the previous study. In addition, there is data for two more years, so this thesis contains data for two years with icing events and two without. I was therefore able to investigate the degree of site fidelity displayed by the reindeer. I was also able to show that the same pattern of home range sizes was shown in the following two years.

4.1 Icing events

The combined data from the field validation, ibuttons and precipitation record showed two winters with icing events, 2009/2010 and 2011/2012, and two winters without icing events, 2010/2011 and 2012/2013. The combination of the data sets leads to a robust determination of winters with icing events. The timing of the icing event cannot be determined with accuracy, but it is less important for the purpose of my study that aggregate range use over entire seasons. Stien et al. (2010) found that icing events were caused by more than 10 mm of precipitation during periods with temperatures above 0°C. This happened in both winters with icing events. There were also days with more than 10 mm of precipitation during the winters without icing events. In 2010/2011, the precipitation came during a warm period, but the probability of the temperature being above 0°C was very low. There were quite a few outliers in the data for ground ice thickness this winter, which could mean that there were local icing events. For 2012/2013 the precipitation did not coincide with a warm period and there were fewer places with local icing.

The winter of 2011/2012 could be deemed more severe than the winter of 2009/2010, as the amount of ground ice measured was twice as much. Stien et al. (2010) found that Svalbard reindeer immediately moved out of the areas affected by icing, but there was no apparent effect of the variation in the severity of the icing events on the displacement distances. In addition, the reindeer avoid areas with ground ice when digging feeding craters when the ice is above a fairly low level. In an area with median ground ice of 9 cm, the

reindeer sometimes cratered areas that contained 0,5 to 1 cm of ice, but most areas were ice free (Hansen et al. 2010a). It appears that reindeer avoid areas with more than 1 cm of ground ice when searching for food. In this study, the average thickness of ground ice during icing years were 3.2 cm and 5.2 cm. Therefore, I argue that there is no need to distinguish between the winters with icing events when calculating significance, as I have done throughout the thesis.

4.2 Home range size

As predicted in P1a, winter home ranges were significantly larger than summer home ranges. The size of winter home ranges during years with icing were significantly larger than during years with no icing events, as predicted in P1b. Tyler and Øritsland (1989) found that Svalbard reindeer have small, seasonal home ranges, unlike reindeer and caribou (*Rangifer tarandus*). The authors stated that the animals are able to find enough forage to sustain them without having to wander far. Their findings also suggested that the reindeer do not move more or further in winter than the other seasons, likely because the cost of movement did not outweigh the benefits of searching for distant food patches (Tyler & Øritsland 1989). Since the animals usually are sedentary, conditions would be very poor to make the animals risk expanding or leaving their home ranges (Tyler & Øritsland 1989). This is confirmed by this study, as the average home ranges during summers and winters without icing events were very similar. It therefore seems that the size of the home range is similar during the summer and winter, unless extreme climatic events cause the reindeer to drastically alter their range use.

Svalbard reindeer have been found to have larger home ranges when habitat quality is low during the winter, as they must cover a larger area to fulfill their foraging needs (Hansen et al. 2009). During the winter of 2006, the low altitude range at Sarsøyra on Svalbard was mostly covered by ice, which led the reindeer to either seek ice free habitat at high altitude, forage on wind swept ridges, or locate ice free micro-habitat (Hansen et al. 2010a). In line with these studies, I found that the reindeer expanded their home range areas when they faced a lower availability of forage due to ground ice. Other ungulates have also been found to have varying home range size during different seasons, in response to forage availability. Winter home ranges were larger than summer home ranges for elk (*Cervus elaphus*) in North America because forage quality and quantity was reduced during winter (Anderson et al. 2005).

Home ranges of resident and migratory Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in Alaska, USA did not differ in size between summer and winter. When forage is restricted during the winter, the deer shift their home ranges, but do not expand them (Schoen & Kirchhoff 1985). The same seems to have been the case in normal winters for Svalbard reindeer. The Svalbard reindeer thus have a different strategy in ice free winters compared to icy winters. To ensure access to enough forage during icing years, the animals expand their home ranges. The likely explanation for this is that black-tailed deer are browsers feeding in the bush layer which to a lower degree is covered by snow and ice compared to Svalbard reindeer feeding on ground vegetation.

There was a significant difference between home range sizes for Svalbard reindeer of different ages. Animals aged four to seven years had larger home ranges than the animals that were younger (2 – 3) and older (8 – 11). The older animals did not have a significantly different home range size compared to the young animals. This was contrary the prediction P3a, stating that younger animals would have larger home ranges than adults. Young roe deer (*Capreolus capreolus*) were found to have 45 % larger home ranges than adults on a yearly scale (Börger et al. 2006). However, age did not affect home range size for moose (*Alces alces*) in Norway (van Beest et al. 2011). I have no explanation for the surprising finding that young and old Svalbard reindeer had smaller home ranges than midlife animals.

There was a strong tendency for animals with calves to have smaller home ranges than reindeer without calves during the calving season, so P3b was partially supported. Female woodland caribou (*Rangifer tarandus caribou*) in Saskatchewan, Canada without calves had larger home ranges than caribou with calves, irrespective of season (Rettie & Messier 2001). Barren female moose in Norway had larger summer home ranges than females with calf at heel (van Beest et al. 2011). In accordance with other ungulates, Svalbard reindeer have smaller home ranges during years when they have calves.

4.3 Site fidelity

Tyler and Øritsland (1989) found that some Svalbard reindeer show fidelity to seasonal home ranges over several years, and that was supported by this study. As predicted in P2a, the overlap of summer home ranges was greater than the overlap of winter home ranges. This has been found for other ungulates as well. Woodland caribou in British Columbia, Canada had higher site fidelity between years to seasonal home ranges during summer than during winter. This is probably due to a predator avoidance strategy, as they are

more vulnerable to predation during the summer and select the same predator refuges year after year (Wittmer et al. 2006). Polar bear predation on Svalbard reindeer are a rare occurrence that have happened during winter or spring (Derocher et al. 2000), but is far too rare to shape the spatial strategies of Svalbard reindeer. The greater site fidelity during the summer is more likely due to a more predictable food base. For caribou in British Columbia, forage predictability is low during early winter, and they displayed little within-season site fidelity during this time (Wittmer et al. 2006). Migratory and resident Sitka black-tailed deer in Alaska, USA use the same summer range every year and have overlapping winter home ranges. They are most restricted during winters with heavy snowfall, and adjust their home range in elevation to access forage (Schoen & Kirchhoff 1985). The Svalbard reindeer had a similar strategy, as their home ranges were larger and overlapped less when there was a shortage of food during winter. They seem to return to previous sites unless food is unavailable. During those times they apparently go to unfamiliar areas, as the overlap for winter home ranges were generally smaller.

Contrary to P2b, there was only a tendency for a difference in overlap of home ranges between icing years and not icing years during winter. This was unexpected, as it would seem likely that the animals return more often to areas used in winters with a relatively stable amount of forage. The most likely cause of this is that not all individuals responded to icing events by expanding the home range. This might be because they already were in the area with the lowest expected presence of ice, or that they did small scale spatial shift and successfully detected sufficient amounts of ice-free vegetation, as documented by Hansen et al. (2010a).

Based on this data, there was not a significant difference in overlap for reindeer of different ages, rejecting P3a. It was expected that older animals would display a higher level of site fidelity, as older animals usually have smaller and more stable home ranges. This is the case for roe deer (Börger et al. 2006; Pettorelli et al. 2003) and migratory caribou (Schaefer et al. 2000). However, for sedentary caribou there was no effect of age on site fidelity (Schaefer et al. 2000). In accordance with this, older Svalbard reindeer did not show higher site fidelity than younger animals.

There was borderline significance for reindeer with calves having a larger home range overlap than females without a calf, supporting P3b. Schaefer et al. (2000) and (Rettie & Messier 2001) found that calving status did not affect site fidelity for caribou. Females with calves are often more sedentary than females without calves (Hiller et al. 2008), and this is also the case for Svalbard reindeer.

5. Conclusions and future perspectives

This study has investigated the space use of female Svalbard reindeer in response to food restrictions, and the effects of age and calving. Svalbard reindeer have larger seasonal home ranges during winters with ice compared to summer and normal winters, due to a lower availability of forage. The reindeer display higher site fidelity for summer ranges than winter ranges, due to higher predictability of suitable foraging sites. Even though a warmer climate may positively affect summer habitats for resident species, warming can decrease the available winter habitats for Arctic *Rangifer* species (Hinzman et al. 2005). Icing events can increase mortality as the travel costs increase, food access is reduced and predation risk is increased. This is especially likely during the spring, when animals are nutritionally stressed (Hinzman et al. 2005). There are two aspects that determine the future for Svalbard reindeer in relation to icing events during the winter. The first is the extent of rain on snow events and spatial extent of icing in the future and the second is the reindeer's response or behavioral plasticity to overcome these events.

There is evidence of a global decline of caribou and reindeer populations caused by anthropogenic and climatic global change (Vors & Boyce 2009). Some researchers are concerned about the future of Svalbard reindeer. Aanes et al. (2002) found that extreme weather with icing events in 1993 severely impacted a reindeer population on Svalbard. If the predicted increase of extreme climate conditions holds true, the reindeer population will be strongly impacted by an increase in icing events (Aanes et al. 2002; Putkonen & Roe 2003). Though it has been suggested that warmer and wetter winters lead to improved foraging conditions for the reindeer (Tyler 2010; Tyler et al. 2008), this has been contradicted by Hansen et al. (2011) and the results of this study. Hansen et al. (2011) found that simulated values for conditions causing icing events were within or close to the observed climatic range, thus making it unlikely that foraging conditions would be improved through a warmer and wetter climate.

There are however indications that the Svalbard reindeer will be able to behaviorally adapt to the changes. Hansen et al. (2010a) found that Svalbard reindeer responded to icing events in different ways. Some moved to higher altitudes while others stayed and located ice free microhabitats or patches (Hansen et al. 2010a). Stien et al. (2010) concluded that unless the icing events are on a large scale, the reindeer will be able to find ice free forage areas. I found that the animals increased the size of their home ranges in response to icing events. This behavioral plasticity can partially buffer current and future changes in winter climate (Hansen et al. 2010a; Stien et al. 2010). However, if the icing events increase spatially

(Putkonen & Roe 2003), there could be a nonlinear effect on survival which would decimate the population once the extent of icing exceed the realistic range of emigration (Stien et al. 2010). Svalbard reindeer display behavioral responses to reduced forage access which should be able to buffer ground icing events, unless they occur on a large spatial scale.

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Appendix

Table 3. Area of kernel home range of female Svalbard reindeer during the winter, with median and average.

Reindeer ID	Area km ² 2009/10	Area km ² 2010/11	Area km ² 2011/12	Area km ² 2012/13
B100	32,91	44,12	63,37	
B101	75,37	65,66	47,31	49,53
B103	82,18	28,83	75,61	
B106	65,01	43,03	50,35	
B123	25,43	23,46	25,48	10,88
B126			15,26	38,61
B129				22,48
B130		18,18	26,53	16,98
B135			25,71	20,35
B140		61,54	80,74	46,98
B148			8,91	
B153		12,82		
B154		29,26	41,63	32,83
B156		26,16	25,10	
B158		25,00	40,24	
B165		23,22	54,70	
B171		31,74	31,04	
B54	44,75	15,31		
B93	44,59	10,72		
B96	45,80	56,60	34,47	
G39	21,01	21,80		
G53	14,15			
G72	98,54	38,46	77,42	
G89	18,35	38,68		
R240c	18,44	18,41	33,41	
R243	38,20	59,05	36,27	12,81
R264			37,13	48,98
R280	13,54	14,84		
W103	45,99	33,98	59,42	28,38
W64	11,79	12,72		
W72	62,95	14,61		
W74	63,13	27,37	40,56	
W91	84,15	24,31		
Y104	14,18	23,25	18,09	18,40
Y105	30,30	12,35		
Y112	64,52	69,55	60,83	
Y117	39,07	42,33	39,56	22,76
Y120		13,06	14,85	15,08
Y92	14,48	19,69	27,00	29,62
Median	39,07	25,00	37,13	22,76
Average	42,75	30,31	40,41	27,64



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